Sensory structures and sexual dimorphism in the harvestman *Dicranopalpus ramosus* (Arachnida: Opiliones)

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Abstract. A survey on sensory organs of both sexes of the harvestman *Dicranopalpus ramosus* classifies structure and frequency of campaniform sensilla, falciform setae, sensilla basiconica, slit sensilla, solenidia, spines, sensilla chaetica, trichomes (simple hairs) and plumose setae. Sensilla are equally distributed on the pedipalp tarsi of both males and females, but females show higher counts of campaniform and falciform setae than males. Females furthermore have about 1000 glandular plumose setae on each pedipalp, that at the same positions in males are replaced by sensilla chaetica. The walking legs of both sexes show a similar distribution of sensory organs, with females showing more sensilla basiconica at the legs I and II and more solenidia on the first pair of legs. Males have a large number of bipterate setae (about 2200 per specimen) at the metatarsi and tarsi of the third and fourth pair of legs. In females these are replaced by simple hairs. Although females show a similar (or slightly higher) number of leg sensilla than males, their density is higher due to their shorter legs. In both sexes the second pair of legs has the largest number of falciform setae, sensilla basiconica, chaetica and solenidia, followed by the legs I, III and IV. The first pair of legs has the highest density of falciform setae, sensilla basiconica and solenidia, followed by the legs II, III and IV. The genital operculum, sternites and tergites show a multitude of slit sensilla. The slit sensilla of the genital operculum and sternites are associated with insertion plaques of muscles operating the penis/ovipositor and regulating opisthosomal volume and hemolymph-pressure.

Keywords: bipterate setae, harvestmen, plumose setae, sensory structures, sexual dimorphism

Zusammenfassung. Sinnesorgane und Sexualdimorphismus der Weberknechtart *Dicranopalpus ramosus* (Arachnida: Opiliones). Im Rahmen einer Untersuchung der Sinnesorgane beider Geschlechter der Weberknechtart *Dicranopalpus ramosus* werden die Struktur und Anzahl der Kuppelsensillen (campaniform), sichelförmigen Borsten (falciforme Setae), Riechkegel (Sensilla basiconica), Spaltsensillen, Solenidien (röhrenförmige Setae) und Dornen sowie der Haarsensillen (Sensilla chaetica), Trichome (einfache Haare) und federförmige Haare (plumose Setae) beschrieben. Die Pedipalpen-Tarsen der männlichen und weiblichen Tiere weisen identische Verteilungen der Sensillen auf, wobei die Weibchen mehr Kuppelsensillen und sichelförmige Borsten besitzen als die Männchen. Weiterhin konnte festgestellt werden, dass auf jedem weiblichen Pedipalpus 1000 gefiederte Drüsenhaare (glandulare plumose Setae) vorkommen, wohingegen bei den Männchen an den gleichen Stellen Haarsensillen vorgefunden werden. Die Beine beider Geschlechter weisen eine ähnliche Verteilung der Sinnesorgane auf, wobei Weibchen mehr Riechkegel in den Beinen I und II und mehr Solenidien am ersten Beinpaar aufweisen. Männliche Tiere besitzen eine große Anzahl zweiflügeliger Borsten (bipterate Setae) (insgesamt ca. 2200 pro Tier) auf den Metatarsen und Tarsen des dritten und vierten Beinpaares . An gleicher Stelle sind bei weiblichen Tieren einfache Haare vorzufinden. Weibchen besitzen eine ähnliche (oder höhere) Anzahl an Beinsensillen als Männchen. Da die Beine der weiblichen Tiere jedoch kürzer sind, stehen die Beinsensillen bei ihnen dichter. In beiden Geschlechtern weisen die zweiten Beinpaare die größte Anzahl an sichelförmigen Borsten, Riechkegeln, Haarsensillen und Solenidien auf, gefolgt von den ersten, dritten und vierten Beinpaaren. Auf den ersten Beinpaaren erreichen die sichelförmigen Borsten, Riechkegel und Solenidien die höchste Dichte, gefolgt von den zweiten, dritten und vierten Beinpaaren. Das Genitaloperculum, die Sternite und Tergite weisen eine Vielzahl von Spaltsensillen auf. Die Spaltsensillen des Genitaloperculums und der Sternite sind mit Muskelansätzen verbunden. Diese Muskeln steuern Penis bzw. Ovipositor und regeln das Opisthosoma-Volumen und den Hämolymph-Druck.

Harvestmen of the suborder Eupnoi primarily gather environmental information with their legs and pedipalps. Eyes are usually small and eyesight in most species is considered to be limited to the ability to distinguish changes in light intensity (Machado & Macías-Ordóñez 2007, Willemart & Hebets 2012).

Walking is accomplished mainly by the first, third and fourth leg pairs. The first and second legs are also used to explore their surroundings, e.g. to find food or a mate. The second – and longest – legs have traditionally been called 'sensory legs', because harvestmen constantly wave them about conspicuously, exploring their surroundings by touch (Goodnight & Goodnight 1976, Hillyard & Sankey 1989). Willemart et al. (2009) stressed that the first legs are also important sensory tools, mainly used for fine recog-

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Fig. 1: A *Dicranopalpus ramosus* male (left) touches a female with the dorsal side of his left pedipalpal tarsus. Understanding intersexual interactions like this requires knowledge of topography and function of sensory organs. Note the dimorphism in pedipalpal proportions and colouration. Photo Jörg Pageler, Oldenburg, Germany.

nition. Thus it might be expected that most sensilla types are located on the appendages and that each leg pair may contain a specific set and density of sensory organs.

Males and females may exhibit differences in sensory organ types and/or densities. Sexually dimorphic structures are usually indicative of a sexual role and often the result of sexual selection (Macías-Ordóñez et al. 2010, Willemart & Giribet 2010). In many Phalangioidea the pedipalps, chelicerae and/or legs are sexually dimorphic; as has been well documented in numerous taxonomic papers (e.g. Martens 1978). Male pedipalps can be modified for clasping the female during mating (many Phalangiidae and Sclerosomatidae; Macías-Ordóñez et al. 2010). Male chelicerae (e.g. *Phalangium opilio* Linnaeus, 1761) can be modified for intrasexual contests (Willemart et al. 2006). In general, legs are longer in males than in females (Martens 1978).

Accounts of sensory biology in harvestmen are scarce, and until now no attempt has been made to depict all sensory structures of one particular species of Opiliones. This study aims at describing and illustrating the diversity and topography of sensory structures (except eyes) of both the male and female of *Dicranopalpus ramosus* (Simon, 1909) – a distinctly sexually dimorphic harvestman – based on light microscopy. Additionally, reproductive structures are described and illustrated.

Dicranopalpus ramosus

The genus *Dicranopalpus* Doleschall, 1852 belongs to the superfamily Phalangioidea (suborder Eupnoi), presently comprising five recognised families: Phalangiidae, Sclerosomatidae, Neopilionidae, Monoscutidae and Protolophidae (Cokendolpher & Lee 1993), as well as a few taxa of uncertain affinities. Mainly because the families are poorly delimited (Giribet et al. 2002, Hedin et al. 2012) the position of *Dicranopalpus* within Phalangioidea is still uncertain. Currently, *Dicranopalpus* belongs to the so called *Dicranopalpus* group, containing seven genera (Crawford 1992, Pinto-da-Rocha & Giribet 2007).

The harvestman *D. ramosus* originates from the Western Mediterranean region (Morocco, Spain, Portugal, southern part of France). Since around 1990 it has been steadily moving north from its original range. Thus far, *D. ramosus* has additionally been recorded from southern England and France (Sankey & Storey 1969), the Netherlands (Cuppen 1994, Noordijk et al. 2007), Belgium (Slosse 1995), Ireland (Cawley 1995), Scotland (Hillyard 2000), Germany (Schmidt 2004) as far north as Denmark (Toft & Hansen 2011), and it has built up stable populations in most of these countries so far as Atlantic climatic conditions prevail.

Adults of *D. ramosus* are primarily arboricolous, living on trees, shrubs and hedges in a wide variety of artificial, semi-natural and natural habitats (Noordijk

et al. 2007). In *D. ramosus*, the colouration of body, chelicerae and pedipalps is sexually dimorphic (Figs. 1, 6), as well as the shape of the pedipalps. The female has shorter legs and develops a distinct dorsal protuberance.

Material and methods

Sources of material – All observations are based on 46 adult males and 53 adult females that were collected by the author in Nijmegen (N: 51°50´20´´, E: 5°52´25´´, ca. 40 m a.s.l.) the Netherlands from 11-x-2011 to 6-xii-2011.

Microscopic preparations – Specimens were preserved in 70% ethanol prior to preparation. For quantitative analyses 10 (left or right) pedipalps, chelicerae or legs of different male and female individuals were randomly selected from the material. The appendages to be studied under the microscope were bisected along their long axis, in the dorsoventral as well as in the mediolateral plane, with a fine surgical razor blade (leg tarsi were not dissected). All inner tissues were then carefully removed by scraping them out using the same blade or a fine pointed wooden toothpick. No staining or clearing was applied. The objects were embedded in water, mounted temporarily on microscope slides, and examined (under oil immersion for magnifications of 400 and 1000x) on an Olympus stereo light microscope (40/100/400/1000x).

Illustrations – All illustrations were based on sketches directly drawn from the microscope with the aid of a calibrated drawing mirror.

Microscopic photography – Objects were cleared in KOH and mounted on microscope slides. Photos were taken with an Olympus BX-40 microscope equipped with an Olympus DP 70 digital microscope camera, using 10x, 20x, 40x and 100x Olympus lenses and transmitted light or phase contrast. Recording of the photographs and length measurements were made using the software Olympus DP Controller 2002 (Olympus Optical Co, Ltd). The software was calibrated to provide proper length measurements. Photographs were enhanced with Adobe Photoshop CS3 software by adjusting contrast and removing small debris particles in the background.

Statistical analysis – To determine if the means of sampled male and female sensory structures were significantly ($p<0.05$) different from one another a two-sample t-test assuming equal variances was used.

Results
Definitions and descriptions of sensory sensilla and setae

Fig. 2 illustrates the sensory sensilla and setae types found in *D. ramosus*. Abbreviations used in illustrations and photos: bas = sensillum basiconicum/sensilla basiconica; bi = bipterate seta/setae; cam = campaniform sensillum/sensilla; ch = sensillum chaeticum/sensilla chaetica; CO = coxa; fal = falciform seta/setae; FE = femur; MT = metatarsus; PA = patella; pl = plumose seta/setae; sl = slit sensillum/sensilla; sol = solenidium/solenidia; sp = spine(s); TA = tarsus; TI = tibia; TRO = trochanter; tr = trichome(s).

Fig. 2: Sensory structures and setae in *D. ramosus* with abbreviations used in figures (right is distal direction). From left to right: 2 spines (sp), 3 trichomes (tr), 2 slit sensilla (sl), 4 sensilla chaetica (ch), 2 solenidia (sol), 1 campaniform sensillum (cam), 3 sensilla basiconica (bas), 1 plumose seta (pl), 2 falciform setae (fal), 2 bipterate setae (bi). Scale bar: 50 μm.
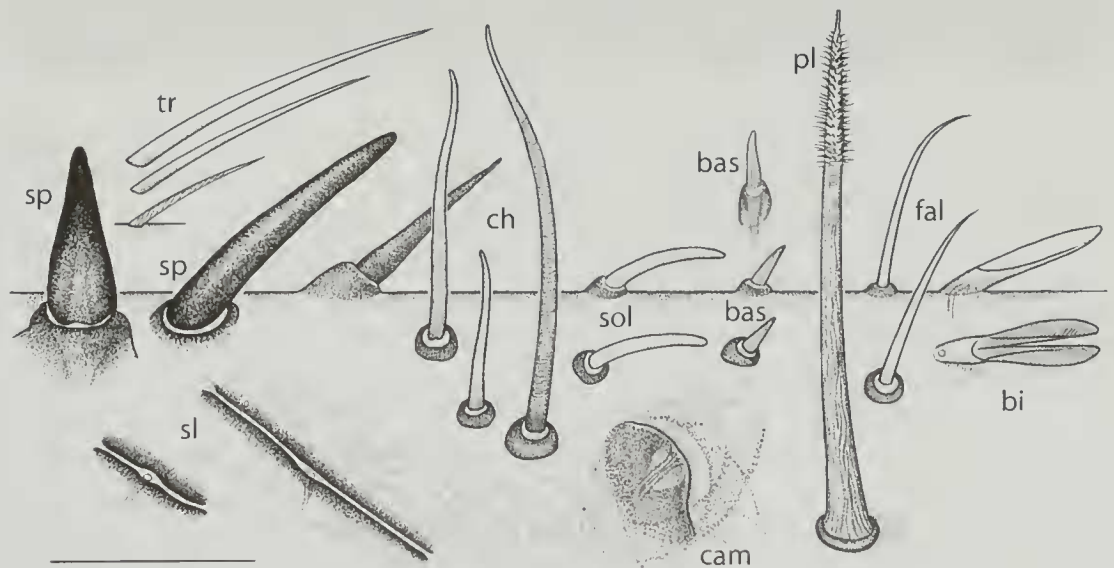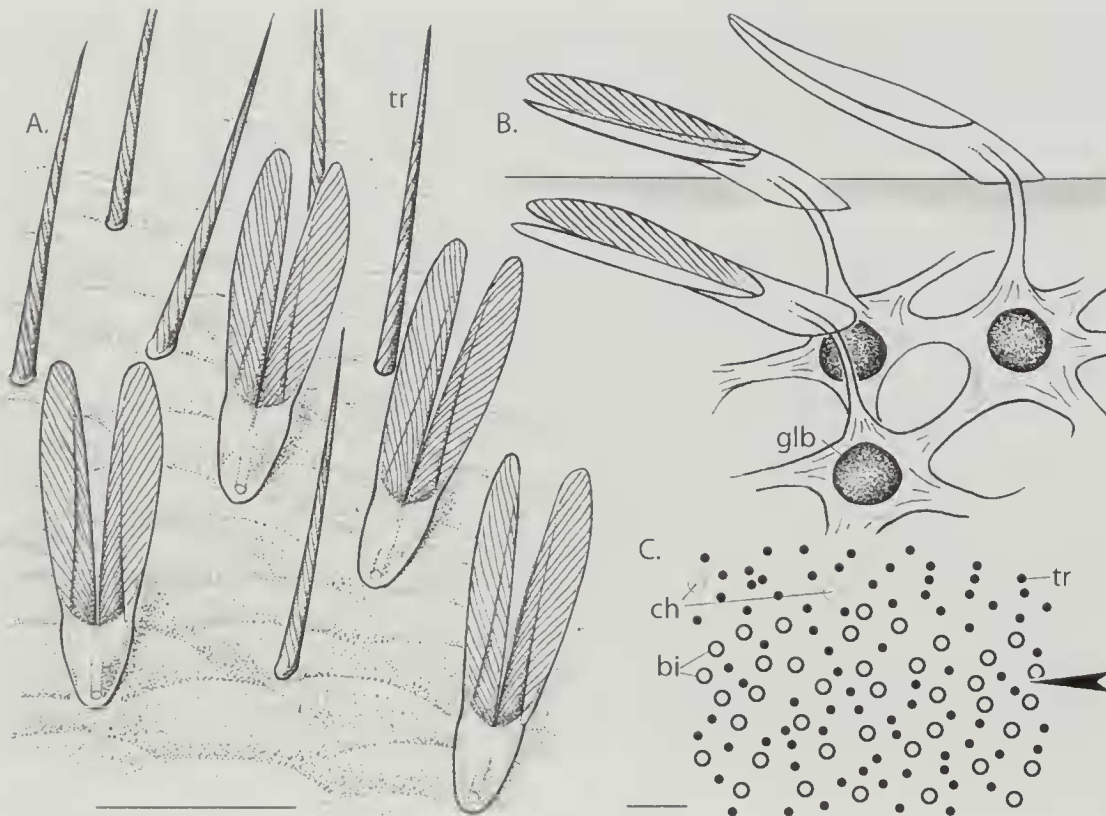
Fig. 3: Bipterate setae in *D. ramosus* dorsally on male metatarsus leg III. A. Trichomes and 4 bipterate setae; B. Diagram of internal structure of bipterate setae with internal globular bodies (glb); C. Topography and density of bipterate setae (large open dots) and trichomes (small dots) on a dorsal section of metatarsus leg III. Top of the figure is the posterior direction, arrow indicates dorsal midline of metatarsus. Scale bar: A, B = 25 μm; C = 50 μm.

Bifid metatarsal spine (Figs. 10a, 11) – A previously unknown type of hair sensillum (see Legs, Metatarsus). It is inserted in a socket membrane and has two fused, dark coloured shafts, one short, with a blunt end (app. 15 μm), the other long and tapering (app. 45 μm).

Bipterate setae (Figs. 2, 3, 5c, 5d, 10) – First mentioned as 'flat setae' by Willemart et al. (2009). A more appropriate new name for this sensillum type ('bipterate' seta) is proposed here, meaning 'double-winged' (while 'flat setae' are defined as flattened, non-bifid setae). The insertion of the short cylindrical shaft is rigid, the shaft widens slightly

towards a distal portion of two delicately striated, concavely curved 'wings'. The angle of insertion is about 25° and the length is approximately 40 μm. Bipterate setae have elaborate internal structures but their description requires more sophisticated microscopic techniques. Fig. 3b illustrates what can be seen with light microscopy. At the junction of shaft and wings each seta seems to have some kind of micropore, which connects via a canal with an internal globular body of unknown substance (in one collected specimen the globular inner structures were clearly discernible because they had turned red as a result of some chemical reaction; later the red
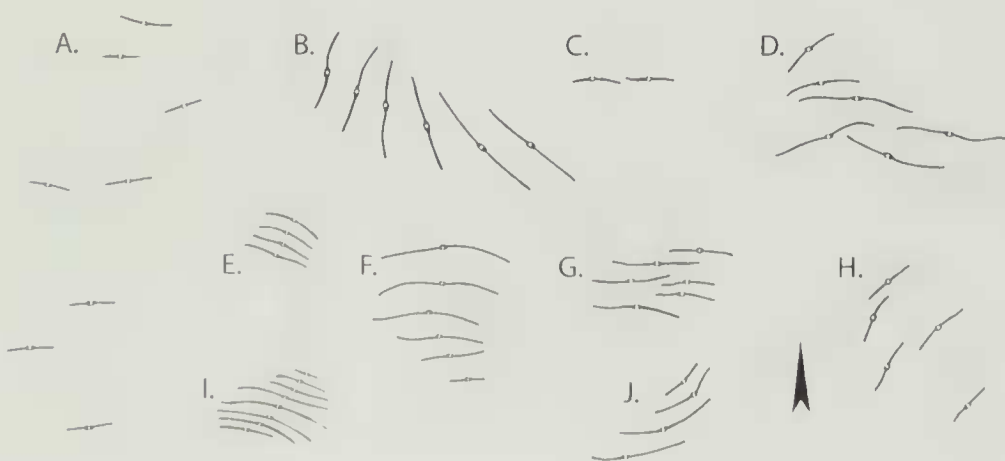

Fig. 4: Slit sensilla groups in *D. ramosus*. A. Male genital operculum, left side; B. Male left chelicera, near the dorsal junction of the second and third segment; C. Female ovipositor, ventral right side; D. Male pedipalpal femur; E. Female trochanter leg I; F. Female coxapophysis leg II; G. Female pedipalpal femur; H. Male left chelicera, first segment; I. Female trochanter leg IV, posterior side; J. Female pedipalpal trochanter. For all slit groups the arrow points towards the distal region of the mentioned body part. Scale bar: 50 μm.
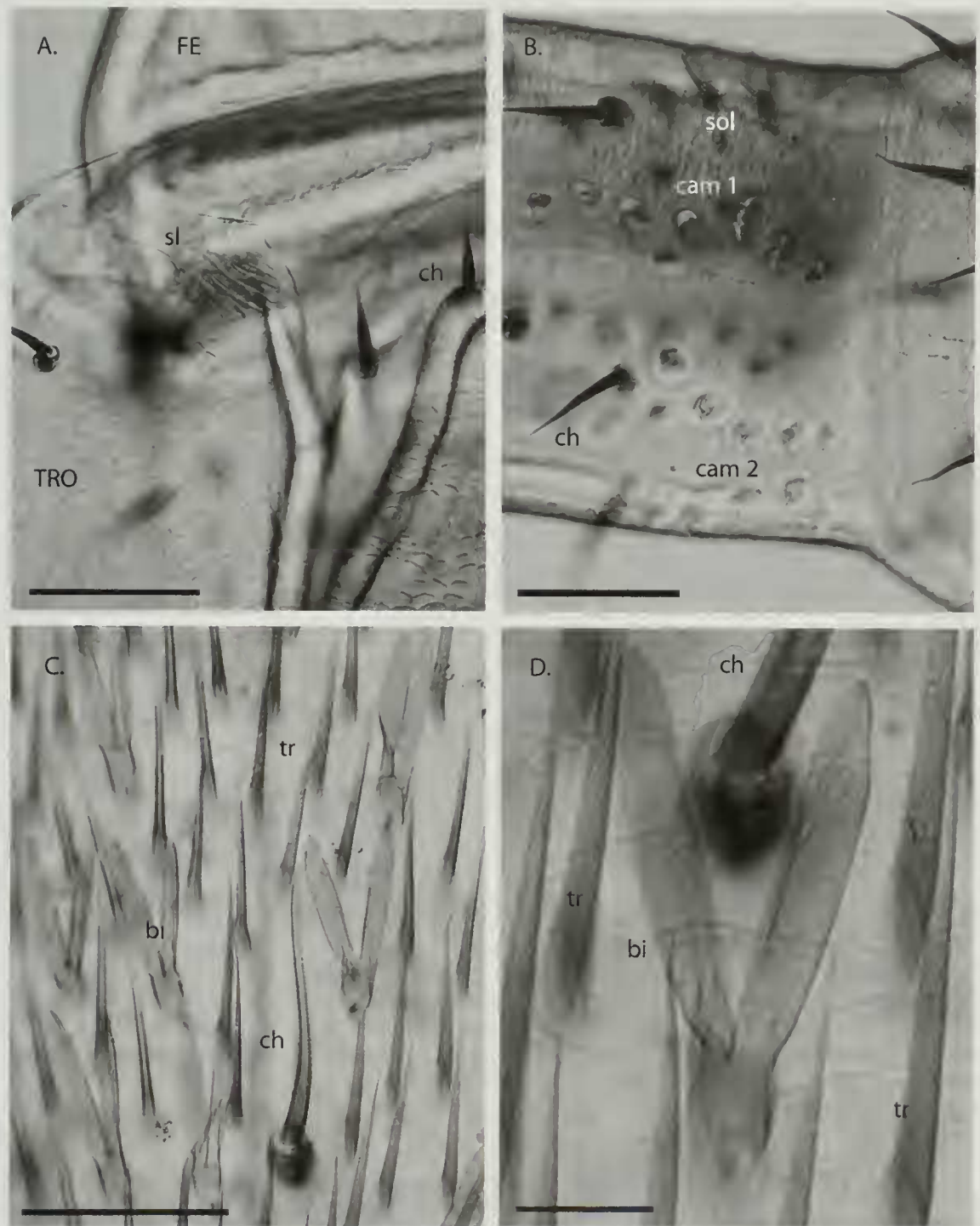
Fig. 5: A. Posterior slit group on trochanter of male leg I. Scale bar 100 μm; B. Proximal region of right male leg III, with an anterior (cam 1) and a V-shaped (cam 2) ventral campaniform sensilla group and 2 solenidia. Scale bar 100 μm; C. Bipterate setae dorsally on metatarsus of male leg III. The sensillum chaeticum has transverse striae. Scale bar 40 μm; D. One bipterate seta, showing striated wings and spirally striate trichomes. Scale bar: 10 μm. Photos Walter Pfliegler (Debrecen, Hungary).

colour vanished). The globular bodies are probably innervated.

Slit sensilla (Figs. 2, 4, 5a, 6-11, 13) – Slit sensilla appear as elongated depressions in the cuticle, the dendrite attachment site in the centre of the slit showing as a transparent 'pore' under the microscope. Also, slits can be surrounded by a dark brown, oval shaped sclerotized zone of exocuticle and frequently the endocuticle is thickened on both sides of the slit. The associated dendritic sheath is often visible. Slits are very small (15 μm) to large (60 μm), and stand isolated or in loose to dense groups of up to 8 slits

depending on their location (Fig. 4). Most slits are oriented approximately perpendicular to the long axis of the appendage.

Campaniform sensilla (Figs. 2, 5b, 7-10) – Campaniform sensilla (also called campaniform organs) are circular to oval structures in the cuticle with a curved slit approximately 15 to 30 μm wide. The light microscopic image reveals details of an inner structure of round or oval shape. This makes them easy to identify, although on the leg metatarsi (Fig. 10) three or four campaniform sensilla occur with a shape approaching that of the slit sensilla. Unlike slit
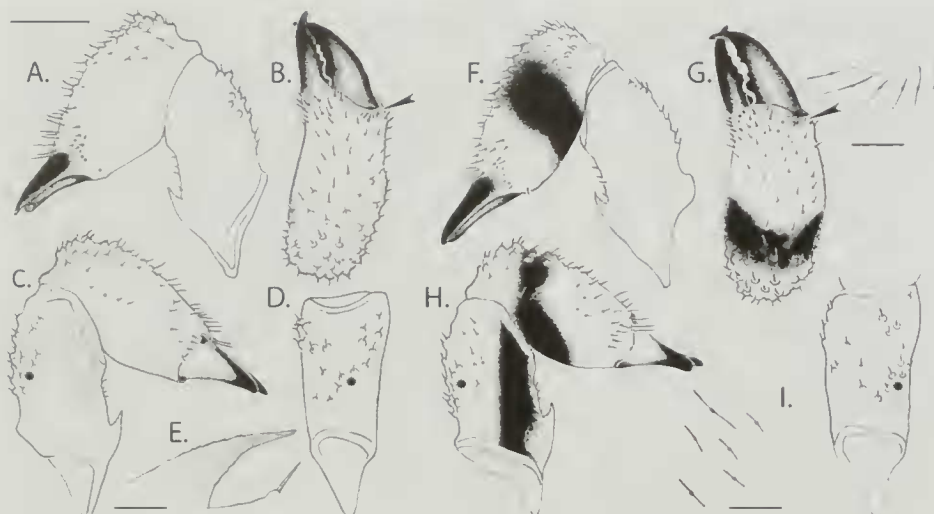
Fig. 6: Right chelicerae of *D. ramosus* showing sensilla chaetica and slit sensilla groups; A-E. Male; F-I. Female. A. Median view; B. Dorsal view of distal portion (arrow indicates location of slit group); C. Lateral view; D. Dorsal view of first cheliceral segment; E. Detail of ventral spur; F. Median view; G. Dorsal view of distal portion and group of slit sensilla associated with the dorsal articulation of the cheliceral finger (arrow indicates location of slit group); H. Lateral view; I. Dorsal view of first cheliceral segment and group of slit sensilla. Asterisk indicates location of slit group. Note sexual differences in colouration. Scale bars: chelicerae (top left) = 0.5 mm; E and slits = 50 μm.

sensilla the campaniform organs have an asymmetrical makeup. Both ends of the curved campaniform slit are always directed proximally, the campaniform slit opening is in the distal region while the dendrite attachment site is on the proximal side (Fig. 2). The campaniform slit is oriented at an angle of 45° to 90° relative to the long axis of the appendage. As with slit sensilla, the campaniform sensilla can stand isolated or in loose to dense groups of up to 10 sensilla.

Sensilla chaetica (Figs. 2, 3, 5-14) – Several varieties were found. They all have in common the fact that the shaft inserts into a large socket membrane. In some cases the seta is placed on top of a tubercle. The angle of insertion is 20° to 90°. On the leg metatarsi, tarsi and pedipalpal tarsi sensilla with highly variable shaft lengths occur (35–120 μm long), with the distal portion often curved upward, extending beyond the trichomes (Fig. 7C); they are transversely striated and appear more transparent than the sensilla chaetica on the leg femora, patellae and tibiae, indicating that they may have thinner shaft walls.

Falciform setae (Figs. 2, 7, 12) – They resemble sensilla chaetica, but are thinner, generally shorter (app. 50 μm) with a fine pointed tip and the basal socket has a smaller diameter. Falciform setae are inserted into the cuticle at an approximate right angle and their shafts are characteristically curved in a distal direction. No striae could be detected. Under the light microscope they appear to be more transparent than sensilla chaetica, suggesting that they have thinner shaft walls.

Plumose setae (Figs. 2, 9) – Glandular setae, rigidly inserted into the cuticle at an approximately straight angle on a heavily sclerotized ring-shaped socket of about 18 μm diameter. Their length is 90–

120 μm. The shaft exhibits rugose longitudinal striae, presumably with some wall pores, although this latter aspect could not be determined with certainty. The plumose distal portion is not striated and is covered with minute hairs. Broken plumose setae reveal a thin shaft wall.

Sensilla basiconica (Figs. 2, 7, 8, 12) – In this contribution sensilla basiconica (also referred to as 'basiconica') are defined as setae with a short, rigid pointed shaft (app. 8–15 μm), inserted into a socket membrane. The angle of insertion is 20° to 90°. Because of their small size, similarity to broken setae and isolated occurrences they are easily overlooked. They also are often obscured by surrounding trichomes. In *D. ramosus* these setae typically appear isolated or in close-set groups of two or three.

Solenidia (Figs. 2, 5b, 7, 8j, 10a, 12c) – Defined as setae inserted within a socket membrane at an angle of 20° to 45°, having an obtuse end ('sausage-like'). They measure about 35 μm and are characteristically curved towards the integument. Also, they appear as transparent, thin-walled setae, whereas most other setae (like sensilla chaetica and trichomes) have thicker walls and as a result appear darker.

Spines (Figs. 2, 8i, 10-12, 14) – Spines are large, heavily sclerotised setae inserted in a socket membrane. One type is robust and blunt (40 μm long; Figs. 2, 8l) another type is more slender (75 μm long; Figs. 2, 8i, 10-12, 14).

Trichomes (Figs. 2, 3a, 3c, 5c, 5d, 7c, 10a, 11) – Hairs without a socket membrane, their shafts insert directly into the cuticle. They measure approximately 40 μm and the angle of insertion is about 20° to 30°. Trichomes show a tendency of being longer and thicker towards the distal regions of the leg meta-
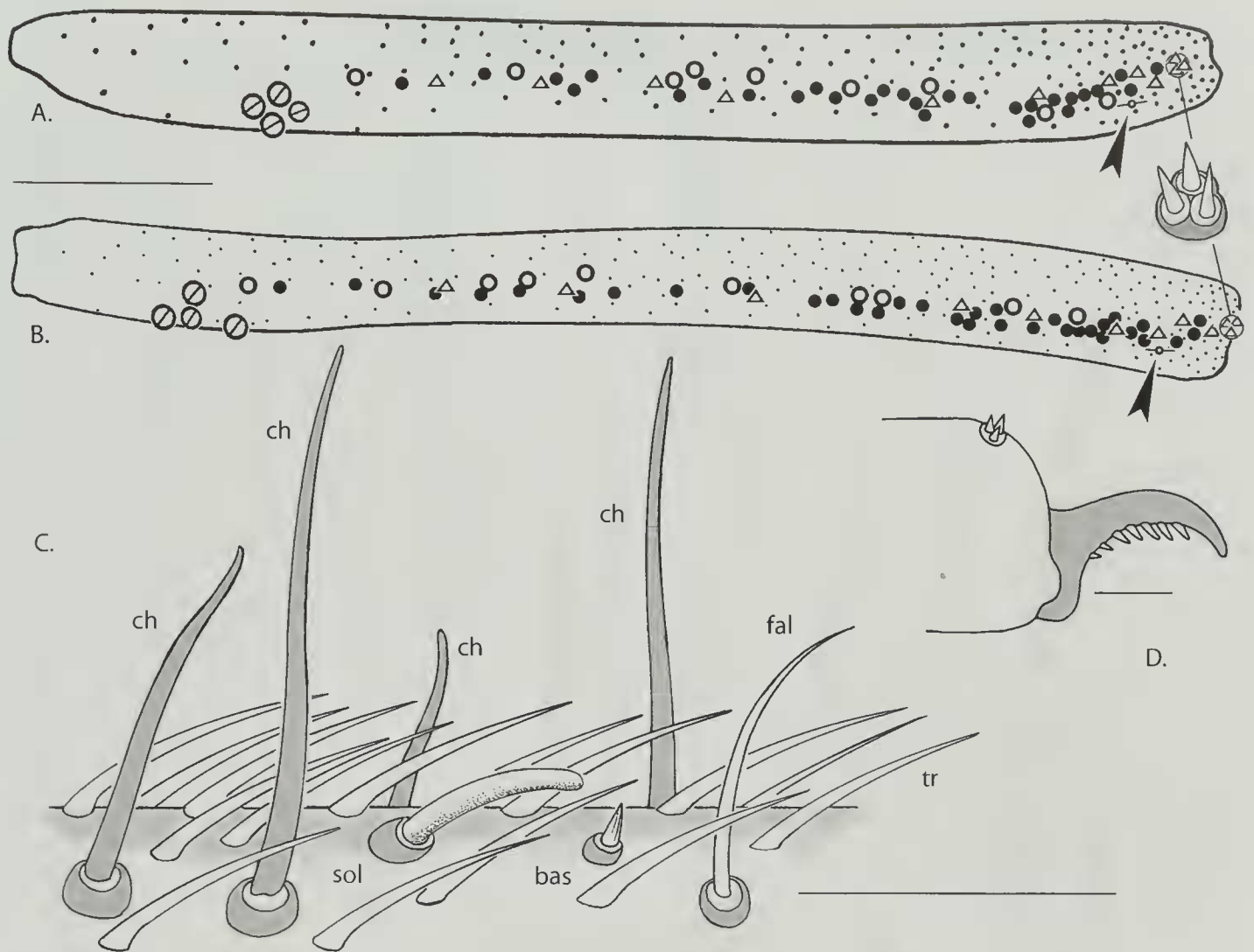
Fig. 7: A. Topography of sensilla on male right pedipalpal tarsus (trichomes not drawn; right is distal direction; based on spread-out dorsal portion of bisected tarsus): campaniform sensilla (large open dots; midline indicates orientation of the slit), falciform setae (open dots), sensilla basiconica (triangles), sensilla chaetica (small dots), solenidia (large black dots), a single slit sensillum proximally of the tip (arrow) and group of 3 basiconica; B. Female pedipalpal tarsus (symbols see A.); C. Diagrammatic representation of dorsal region of left pedipalpal tarsus (right is distal direction) showing 4 sensilla chaetica and one falciform seta extending beyond the trichomes, whereas the solenidium and sensillum basiconicum are concealed within a dense cover of trichomes; D. Lateral view of palpal tarsus with pectinate claw and location of distal basiconica group (other sensilla not drawn). Scale bars: A, B = 0.25 mm; C, D = 50 µm.

tarsomeres and tarsomeres, with maximum lengths of about 90 µm. At the ventral sides of the distal leg tarsomeres trichomes form a brush-like, dense cover of long, often curved sctae. The shafts of some trichomes are distinctly spirally striate (Figs. 2, 3, 5d).

Distribution of sensilla on the appendages
Chelicerae
Male chelicera (Figs. 4b, 4h, 6, 13a) — Basal segment with ventral spur (Figs. 6c, e). The only type of seta present is the sensillum chaeticum, occurring mainly on the dorsal, lateral and median sides; dorsally placed on top of a tubercle. The longest sensilla chaetica are located near the gap, proximally of the

cheliceral fingers. At the articulation of the movable finger the second segment has a group of 6 slits (Figs. 4b, 6b). This represents the slit group with the longest slits found in *D. ramosus*. On the basal cheliceral segment a group of 5 or 6 small slit sensilla is located, in a dorsolateral position (Figs. 4h, 6d) set at an approximate angle of 45° relative to the long axis of the appendage.

Female chelicera (Figs. 6f-i) — Arrangement of slit groups and sensilla chaetica as in the male.

Pedipalps
In both sexes the pedipalps are characteristic in that they have a small apophysis near the ventral base

Tab. 1: Mean numbers, standard deviation and range of four sensory structures on the pedipalpal tarsus of *D. ramosus* (n = 10 males, 10 females). Numbers in bold represent significant differences (p<0.05).

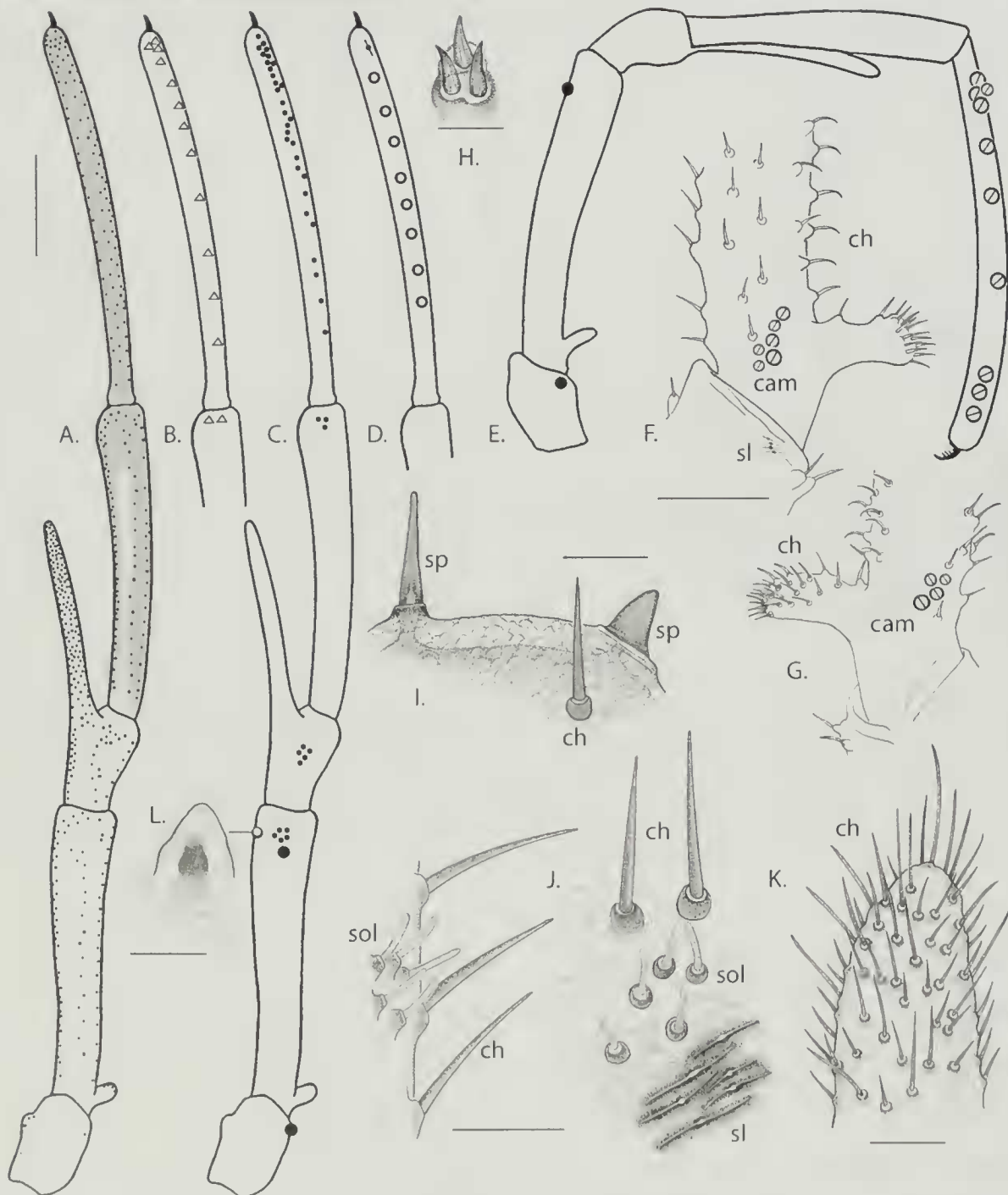| Sensillum type	Male			Female			t-test
	Mean	SD	Range	Mean	SD	Range	P
Campaniform sensillum	10.2	1.33	8-12	15.4	0.92	14-17	**<0.001**
Falciform seta	9.6	1.02	8-11	12.5	1.02	10-14	**<0.001**
Sensillum basiconicum	11.3	1.19	10-14	11.3	0.78	10-12	0.84
Solenidium	31.0	1.79	29-34	32.4	1.20	30-34	0.07

Fig. 8: Topography of trichomes and sensilla types on male pedipalp *D. ramosus*; A-D. Dorsal view of right pedipalp. A. Trichomes (grey area) and sensilla chaetica (dots); B. Sensilla basiconica; C. Solenidia (small dots) and two slit groups (large dots); D. Falciform setae and single slit sensillum near the tip; E. Lateral view of right pedipalp with slit groups (black dots) and campaniform sensila (open dots, midline indicates orientation of slit; slits not drawn to scale); F. Lateral view of trochanter with slit group, and proximal region of femur with sensilla chaetica and 6 campaniform sensilla; G. Median view of femur with sensilla chaetica and 4 campaniform sensilla; H. Group of 3 close-set sensilla basiconica dorsodistally on tarsus; I. Distal margin of femur; J. Solenidia associated with a slit group, and sensilla chaetica on femur, lateral view (left; slits not visible), dorsal view (right); K. Tip of patellal apophysis; L. Blunt spine-like projection. Scale bars: A-E (vertical bar) = 0.5 mm; F, G = 0.25 mm; H = 12 µm; I-L = 50 µm.

Fig. 9: Topography of trichomes, plumose setae and sensilla types on female pedipalp *D. ramosus*; A-D. Dorsal view of right pedipalp. A. Trichomes (light grey area) and sensilla chaetica (dots); B. Sensilla basiconica; C. Solenidia (small dots), plumose setae (dark grey area) and two slit groups (large dots); D. Falciform setae and single slit sensillum near the tip; E. Median view of right pedipalp with plumose setae (grey area); F. Lateral view of right pedipalp with slit groups (large dots), plumose setae (grey area) and campaniform sensilla (open dots, midline indicates orientation of slit; slits not drawn to scale); G. Lateral view of trochanter with slit group, and proximal region of femur with sensilla chaetica, plumose setae and 6 campaniform sensilla (open dots); H. Median view of proximal femur with sensilla chaetica, plumose setae and 5 campaniform sensilla; I. Plumose setae on patellal apophysis; J. Left: a plumose seta, right: lateral view of proximal part of plumose seta with glandular channel; K. Blunt spine-like projection. Scale bars: A-F = 0.5 mm; G, H = 0.25 mm; I, K = 50 μm; J = 25 μm.
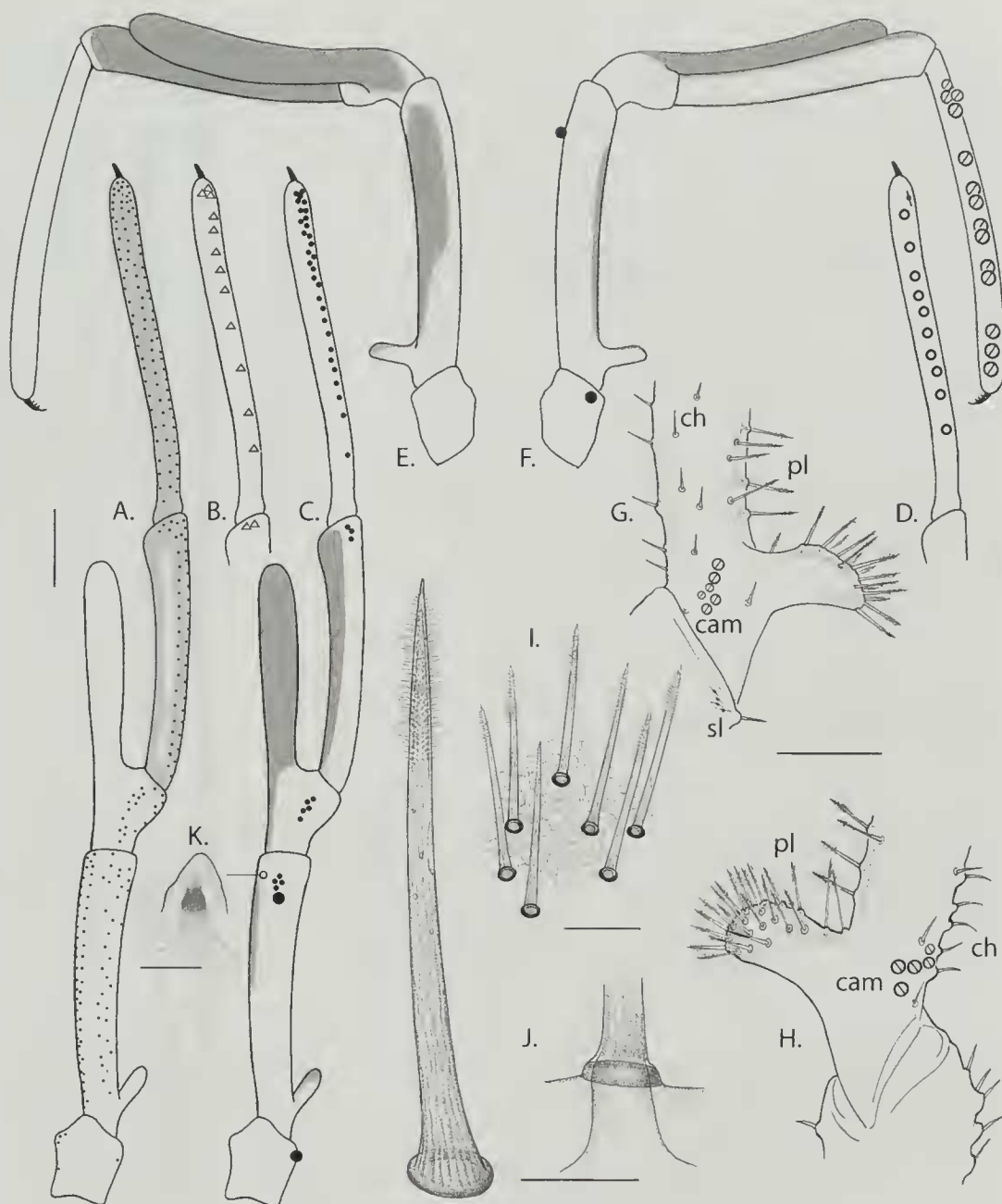
of the femur and an extremely elongated apophysis on the median side of the patella. The pedipalps are highly sexually dimorphic

Male pedipalp (Figs. 7a, 8; Tabs. 5, 6) – Length 6.5 mm (6.2–6.8 mm; SD = 0.24; n = 10). One group of 4 slit sensilla laterodistally on the trochanter (Figs. 8c, e, f). One campaniform sensilla group (4 to 6 sensilla) at the median and one at the lateral base of the femoral apophysis (Figs. 8f, g). Distal region of femur with a group of 5 or 6 slits, accompanied by 4 or 5 solenidia (Fig. 8j). At the medial side of this slit/solenidia group an unidentified blunt, spine-like structure occurs (Fig. 8l). A group of 4 or 5 solenidia dorsally on the patella (Fig. 8c). The patellal apophysis is slender and pointed, densely and exclusively covered with sensilla chaetica of various lengths (Figs. 8a, k). The

pedipalpal tarsus has a particularly rich assortment of sensory types. Among a cover of trichomes, numbers of basiconica, solenidia, falciform setae, campaniform sensilla and sensilla chaetica occur and close to its tip there is a single slit sensillum. Their distributions are shown in Fig. 7. The falciform setae comprise one irregular dorsal row. More to the dorsolateral side the basiconica and solenidia are arranged, with higher concentrations towards the tarsal tip. Campaniform organs are present as a group of 3 to 4 sensilla on the dorsolateral proximal region and as more or less isolated ones along the lateral (posterior) side of the tarsus (Figs. 7a, 8e). At the most dorsodistal tip of the pedipalpal tarsus a group of 3 close-set sensilla basiconica is located (Figs. 7a, d, 8b, h). No ventral row of spines on the tarsus. Pedipalpal claw pectinate
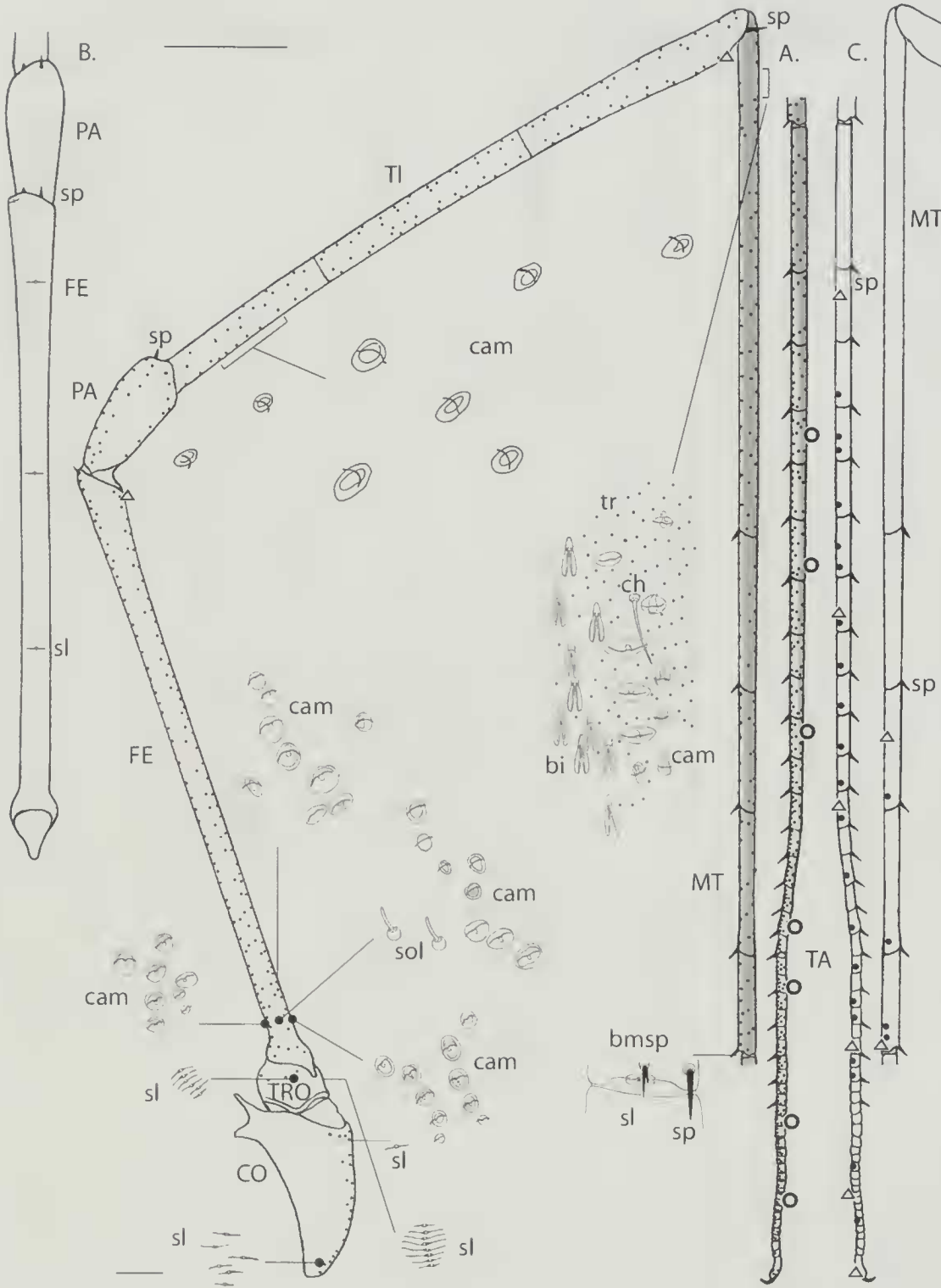
Fig. 10: Topography of sensory structures *D. ramosus* male left leg III. A. Anterior view with spines, sensilla chaetica (small dots), bipterate setae (grey area), falciform setae (open dots), 2 sensilla basiconica (triangle) and an isolated slit sensillum accompanied by a bifid metatarsal spine (bmsp); B. Dorsal view of left femur and patella showing spines and single slits; C. Posterior view of metatarsus and tarsus with sensilla basiconica (triangle) and solenidia (black dots). Orientation of details of campaniform sensilla groups and slit groups in direction of leg position. Some examples of spines (sp) are given. Scale bars: A-C (top) = 1 mm; details (bottom) = 50 μm.

(Fig. 7d). Tab. 1 summarises the numbers of sensilla on the pedipalpal tarsus.

Female pedipalp (Figs. 7b-d, 9; Tabs. 5, 6) – Length 6.8 mm (6.6-7.0 mm; SD = 0,13; n = 10). Topography of basiconica, solenidia, trichomes and falciform setae similar to the male. A distinctly sexually dimorphic feature is the large and rounded patellar apophysis. It is completely and densely covered with approximately 700 plumose setae (Fig. 9). No other sensilla types are

found on the apophysis. Plumose setae also occur on the femoral apophysis (Figs. 9g, h), the median areas of the femur and tibia; total numbers per pedipalp exceed an estimated 1000. Within the plumose areas of the patella and tibia no sensilla chaetica appear. In all females examined, most of the distal plumose setae regions are partly covered with coagulated droplets or completely covered with a translucent sticky secretion. Cross sections of the patellar apophysis show that the plumose
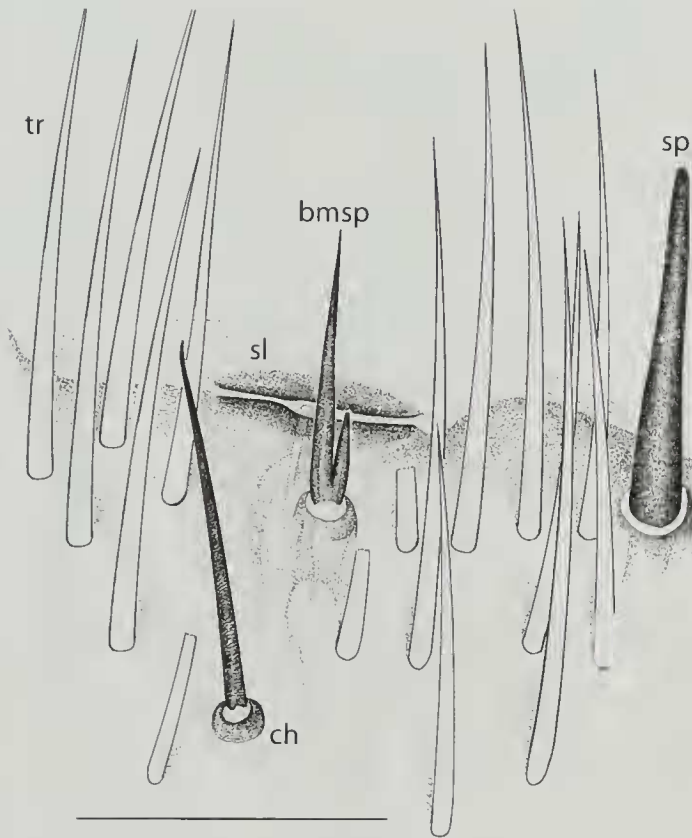
Fig. 11: Ventrodistal margin of metatarsus female right leg III with sensillum chaeticum, trichomes (some not drawn completely), one anterior spine, a single slit sensillum and a bifid metatarsal spine (bmsp). Scale bar: 50 μm.

Fig. 12: Tarsomeres of left leg (trichomes not drawn). A. 15th tarsomere male leg I, anterior view, with many sensilla chaetica of the short type at its ventral side; B. 15th tarsomere male leg IV, anterior view; C. Diagrammatic posterior view of a tarsomere leg I, illustrating the most frequent topography of sensilla basiconica and solenidia. Scale bar: 50 μm.

setae are connected with internal glands, containing a yellowish secretion. The patellal apophysis can essentially be regarded as one large gland. Internal glandular tissues are also present in the femur and tibia.

As in the male there is a dorsal group of 3 close-set sensilla basiconica near the tip of the female pedipalpal tarsus and a single slit sensillum (Figs. 7b, d). The pedipalpal tarsus has 14 to 17 campaniform sen-
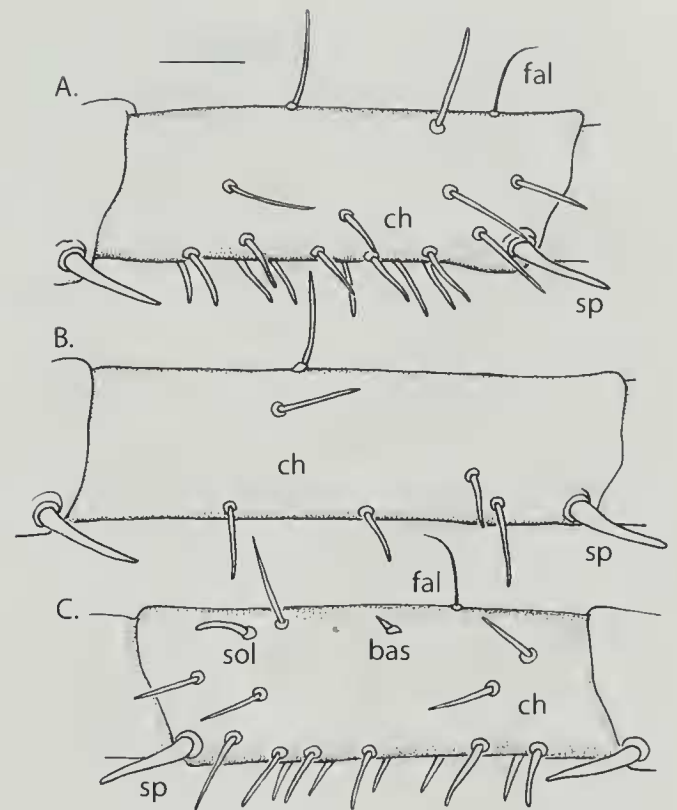
silla, with a proximal group of 4 or 5 and a distal one of 3, whereas the in-between sensilla are frequently arranged in pairs (Fig. 9f). Tab. 1 summarises the numbers of sensilla on the pedipalpal tarsus.

Legs

The tibia, metatarsus and tarsus have a variable number of pseudoarticulations or segments (Tab. 2). Male

Tab. 2: Mean leg lengths [mm] and standard deviation of 10 males and 10 females of *D. ramosus*. In parentheses the numbers of pseudoarticulations (tibia) or segments (metatarsus and tarsus).

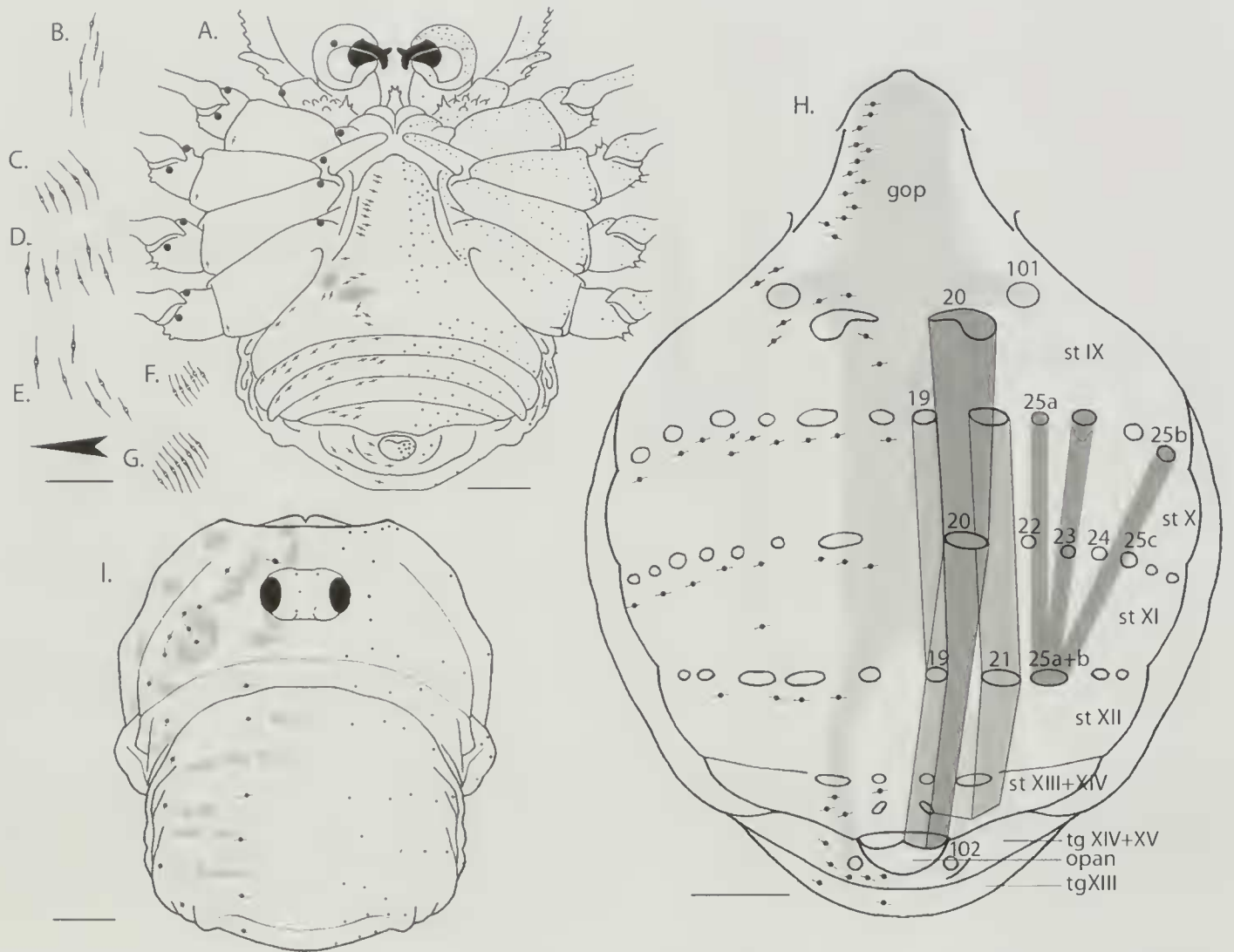|		FE	PA	TI	MT	TA	Leg length	SD
Male leg nr.	I	5.9	1.2	6.3 (3-5)	8.6 (6-10)	8.8 (44-51)	30.7	1,72
	II	9.6	1.3	10.8 (7-10)	12.8 (11-16)	23.3 (86-93)	57.8	2,28
	III	5.1	1.2	5.4 (2-4)	8.4 (4-7)	9.7 (50-54)	29.8	1,12
	IV	6.9	1.2	7.4 (4-5)	11.4 (7-9)	13.5 (55-61)	40.4	2,00
Female leg nr.	I	4.7	1.0	5.0 (3-5)	6.4 (4-6)	7.3 (40-49)	24.4	1,63
	II	8.0	1.1	9.3 (7-10)	10.1 (10-13)	19.0 (75-90)	47.5	1,34
	III	4.2	1.0	4.5 (2-4)	6.1 (4-6)	7.5 (50-53)	23.3	2,10
	IV	5.8	1.0	6.3 (3-4)	9.1 (6-9)	11.3 (47-59)	33.5	1,45

Fig. 13: Topography of sensory structures on body of *D. ramosus* (slits not drawn to scale). A. Male ventrum, chelicera, coxae and trochanters. Right side: sensilla chaetica (dots); left side: isolated slits (small black line with dot) and slit groups (large black dots). Grey spots correspond with insertion plaques of anterior extrinsic penial muscle (101) and lateral longitudinal muscle (20; see H); B-G. Slit groups (arrow indicates distal appendage direction) of: B. Coxapophysis leg I; C. Coxapophysis leg II; D. Coxa leg III; E. Coxa leg IV; F. Trochanter leg II anterior side; G. Trochanter leg II posterior side; H. Combined diagrammatic view of female genital operculum and ventrum with slit sensilla and muscle insertion plaques (numbers according to Shultz 2000). Left side: slit sensilla. Right side depicts dominant longitudinal muscle groups. Light grey area in the background indicates position of pregenital chamber and genital muscles with insertion plaques of anterior (101) and posterior extrinsic genital muscles (102). Abbreviations: gop = genital operculum, opan = anal operculum, st = sternite, tg = tergite; I. Male dorsum. Right side: sensilla chaetica (dots); left side: isolated slits and some muscle insertion plaques (grey shapes). Scale bars: A, H, I = 0.5 mm; B-G = 50 μm.

leg III was chosen to illustrate the basic topography of leg sensilla (Fig. 10). Both sexes have the following architecture. Spines occur in pairs on the dorsodistal margins of the femur, patella and tibia, ventrodistal margins of metatarsal pseudoarticulations and proximal tarsomeres of legs I, III and IV (Tab. 3), whereas leg II has no ventral spines (except for the distal metatarsomere, see below). Sensilla chaetica are distributed in large numbers on all leg segments, especially on the ventral sides of the tarsi. Trichomes are present from the patella to the tip. In the ventral region of the distal app. 20–25 tarsomeres trichomes form a dense brush.

Coxa – Coxapohysis of legs I and II, proximal region of coxae III and IV with slit group, a single slit near the posterolateral coxa-trochanter joint of all leg coxae (Figs. 10, 13a-e).

Trochanter – Two slit groups, a small one of 6 slits at the proventral articulating joint with the femur, and a larger one of 8 slits near the retrolateral articulation (Figs. 13f, g).

Femur – Proximally with four groups of campaniform sensilla. The dorsal, prolateral and retrolateral group are irregularly arranged, each consisting of 8 (occasionally 6 or 7) sensilla, the ventral group (Figs.
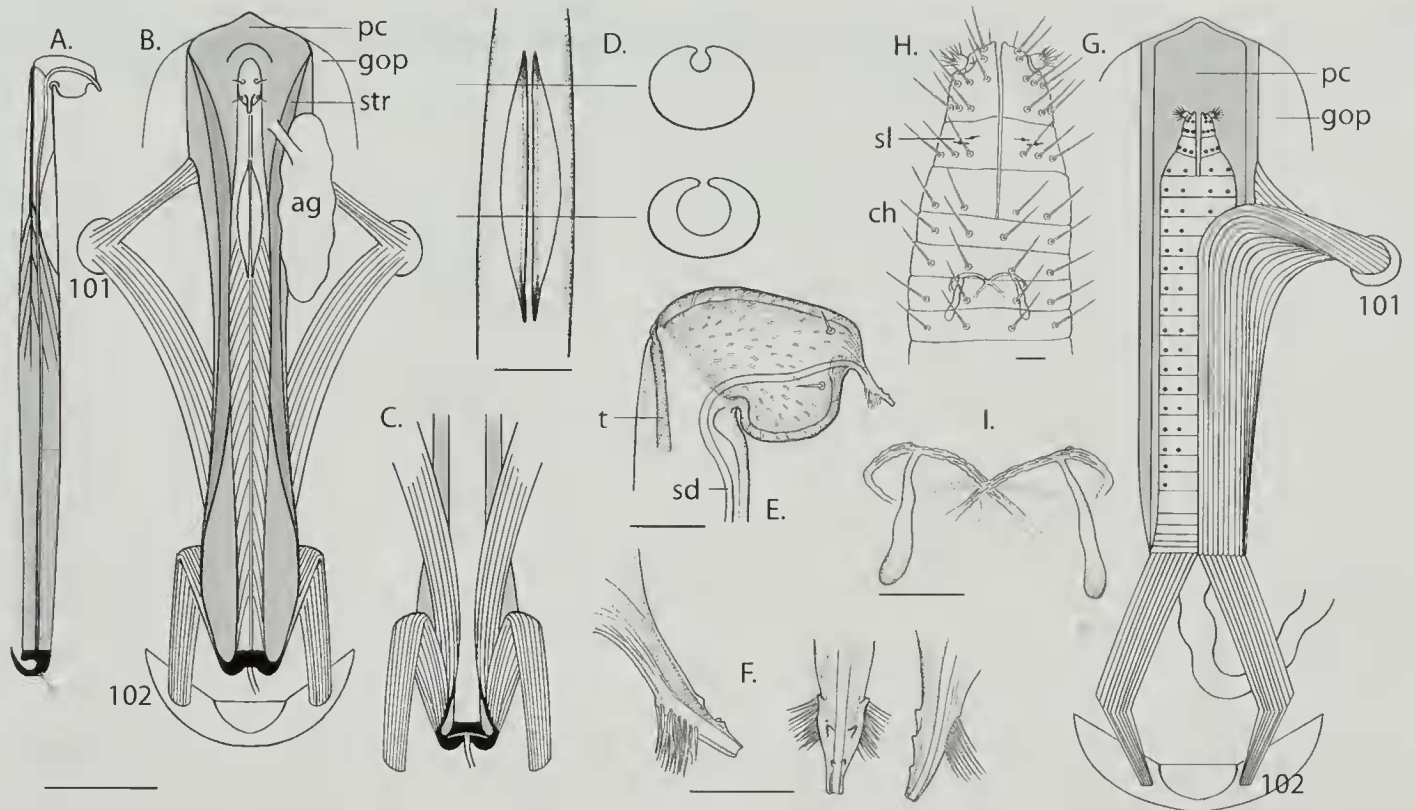
Fig. 14: Reproductive structures of *D. ramosus*. A-F: Male, G-I: Female. A. Diagrammatic lateral view of penis; B. Diagrammatic dorsal view of the genital apparatus with penial muscles and one accessory gland (propulsary organ and gonads omitted); C. Diagrammatic ventral view of the genital apparatus showing extrinsic penial muscles; D. Truncus slit and 2 cross sections; E. Lateral view of glans; F. Lateral and dorsal view of stylus; G. Diagrammatic dorsal view of ovipositor (black dots: sensilla chaetica), pregenial chamber and extrinsic genital muscles (gonads omitted); H. Distal part of ovipositor with sensilla chaetica and two pairs of slit sensilla; I. Seminal receptacles. Numbers indicate muscle insertion plaques (see Fig. 13). Abbreviations: ag = accessory gland, gop = genital operculum, pc = pregenital chamber, str = stiffening rod, sd = seminal duct, t = tendon of intrinsic penial muscle. Scale bars: A-C and G = 0.25 mm; D = 0.1 mm; E, H, I = 50 µm; F = 25 µm.

5b, 10a) consists of 10 campaniform sensilla placed in a 'V' or ')(' shape. All slits of the campaniform sensilla are oriented approximately perpendicular to the long axis of the leg. At the prolateral side of the dorsal femoral group 2 to 3 solenidia appear and occasionally 1 or 2 solenidia at the retrolateral side of the dorsal campaniform group. The femur has heavily sclerotised isolated large slits dorsally, perpendicular to the long axis, more or less evenly spaced: 3 in legs I, III and IV, 6 in leg II (Fig. 10b). One large slit is located at the distal retrolateral articulating joint with the patella. At the ventrodistal margin there is a single sensillum basiconicum.

Patella – Provided with trichomes, sensilla chaetica and two spines (Figs. 10a, b).

Tibia – Ventral proximal side with a group of 8 widely spaced campaniform sensilla (Fig. 10a). Two spines distally. At the ventrodistal margin a single sensillum basiconicum.

Metatarsus – Dorsal proximal region with 10 (occasionally 9) campaniform sensilla more or less in a

row of five pairs. A few sensilla basiconica (2–5) and solenidia (2–6) dorsally. The dorsodistal metatarsal area has one or two sensilla basiconica and one to three solenidia. At the ventrodistal margin a single slit sensillum occurs and proximally of this slit a single bifid metatarsal spine is located (Figs. 10a, 11). The short shaft of the spine is always oriented anteriorly. It occurs in all legs in both sexes.

Tarsus – Large numbers of sensilla chaetica of different lengths on all sides of the tarsomeres. The ventral regions have concentrations of the short type, especially in legs I and II (Fig. 12). The numbers are given in Tab. 3 (for one male and one female all chaetica on the anterior sides of the leg tarsi were counted). The proximal segments have ventral pairs of spines (absent in leg II). Dorsally with solenidia, basiconica and falciform setae (Tab. 3). The sensilla are located at similar sites as in the pedipalp: falciform setae have a strict dorsal position, basiconica and solenidia generally are placed on the dorsolateral side. The majority of the solenidia are located in the

Tab. 3: Mean numbers, standard deviation and range of five sensory structures on the leg tarsi of *D. ramosus* (n = 10 males, 10 females; sensilla chaetica: n = 1 male, 1 female; prolateral side of tarsus). Also sensilla densities are given (in numbers per mm tarsus length). Numbers in bold represent significant differences (p<0.05).

Sensillum type	Leg nr.	Male Mean	SD	Range (numbers)	Density [n/mm]	Female Mean	SD	Range (numbers)	Density [n/mm]	t-test p
Falciform seta	I	13.1	2.13	11-18	1.5	14.2	0.87	13-16	1.9	0.14
	II	16.7	2.54	14-22	0.7	16.9	1.04	16-19	0.9	0.82
	III	7.8	1.48	6-11	0.8	8.2	0.79	7-9	1.1	0.46
	IV	6.4	1.51	4-9	0.5	6.5	1.08	5-8	0.6	0.89
Sensillum basiconicum	I	4.3	0.48	4-5	0.5	6.4	0.97	5-8	0.9	**<0.001**
	II	9.2	1.87	6-11	0.4	12.6	1.12	11-15	0.7	**<0.001**
	III	3.5	1.81	2-8	0.4	4.0	0.67	3-5	0.5	0.46
	IV	5.1	1.44	4-8	0.3	5.3	1.01	4-7	0.5	0.72
Sensillum chaeticum (n=1M, 1F)	I			385	44			279	38	
	II			712	31			592	31	
	III			305	31			246	33	
	IV			265	19			196	17	
Solenidium	I	31.2	2.35	29-37	3.6	37.0	3.27	30-40	5.1	**<0.001**
	II	51.8	4.21	47-59	2.2	50.6	3.38	47-58	2.7	0.49
	III	17.9	2.81	15-23	1.8	20.1	3.03	18-27	2.7	0.10
	IV	14.6	2.55	11-20	1.1	14.4	1.51	14-18	1.3	0.83
Spine (pairs)	I	14.1	3.14	9-18		13.7	2.15	11-18		0.75
	II	-	-	-		-	-	-		-
	III	20.7	1.68	19-24		20.3	1.25	18-22		0.51
	IV	30.5	2.64	26-34		27.4	2.07	23-30		**<0.01**

distal region of the tarsomeres, while the basiconica and falciform setae have a variable proximal/distal position (Figs. 12a, c).

Male legs – The species shows sexual dimorphism in lengths of the legs, in that all male legs are significantly (p<0.001) longer than the female legs (Tab. 2). Male leg III has large numbers of bipterate setae (an estimated 1000) on the metatarsus and proximal 14 to 18 tarsomeres. Bipterate setae are more or less evenly spaced on the prolateral to dorsal surface (Fig. 3c), while in more distal direction they tend to become confined to the dorsal side. Leg IV also has bipterate setae in the distal region of the metatarsus and proximal 8 to 10 tarsomeres (about 100 to 110 bipterate setae per leg). Tab. 3 provides the numbers of tarsal sensilla. The approximate densities of sensilla on the leg tarsi are given as numbers per mm. Tabs. 5 and 6 summarise results concerning sexual dimorphism.

Female legs – Distributions of sensory structures as in the male. Leg lengths (Tab. 2), numbers of tarsal sensilla and densities in Tab. 3. Bipterate setae are absent, instead only trichomes occur (Tab. 6).

Distribution of sensilla on ventrum and dorsum

The ventral side of the body is, in both sexes, provided with sensilla chaetica and slit sensilla (Fig. 13a). Slit groups are present on the pedipalpal trochanters (see Pedipalps; Figs. 8, 9), coxapophyses of legs I and II, proximal leg coxae III and IV and on all leg trochanters (see Legs; Figs. 13a, f, g). Close to the posterolateral coxa-trochanter joint of all legs an isolated slit occurs. Widely spaced, very small slits (15–20 µm) are located near the lateral margins of the genital operculum (11–15 slits per side). Additionally, in both sexes there are small isolated slits on all sternites (total numbers counted: 70 slits each in one female and in one male). A combined representation of sternal slit sensilla, muscles and insertion plaques of ventral muscle groups is presented in Fig. 13h (numeration of muscles and insertion plaques according to Shultz 2000).

The dorsal side of the body also has sensilla chaetica and slit sensilla (Fig. 13i). A pair of large slits is located in front of the eye tubercle, 7 or 8 small slits on both sides of the prosoma are associated with in-

Tab. 4: Mean numbers of slit and campaniform sensilla (arranged as occurring from proximally to distally on the appendage; slit groups in bold text, isolated slits in normal text) and total numbers for one male and one female (in parentheses the differing female numbers are given).

	Slit sensilla	Total	Campaniform sensilla	Total
Chelicera	**6-6**	24	-	-
Pedipalp	**4-5**-1	20	5-5-10 (5-5-15)	40 (50)
Leg I	**6**-1-**6-8**-4-1	52	10-8-8-8-8-10	104
Leg II	**5**-1-**6-8**-7-1	56	10-8-8-8-8-10	104
Leg III	**6**-1-**6-8**-4-1	52	10-8-8-8-8-10	104
Leg IV	**6**-1-**6-8**-4-1	52	10-8-8-8-8-10	104
Dorsum	60	60	-	-
Ventrum	94	94	-	-
Ovipositor	- (**2-2**)	- (8)	-	-
Total male (female)		410 (418)		456 (466)

sertion plaques of the prosomal muscle groups. Tergites VI to XIII have 4 slits, and tergite XIV+XV has about 10 slits associated with the insertion plaques of the posterior extrinsic genital muscles (Figs. 13a, h). A total number of 58 to 60 dorsal slit sensilla was found (n = 2 males, 1 female). Numbers and topography are similar in males and females (Tab. 4).

Reproductive structures

The male and female reproductive organs are homologous structures, located under the genital operculum. These have a characteristic phalangioid morphology (Macías-Ordóñez et al. 2010, Martens et al. 1981). The male genital apparatus (Figs. 14 a-f) comprises a tubular, sclerotized penis and membranous hematodocha, with a dorsoventral pair of large stiffening rods. The penis is long and slender with a large intrinsic penial muscle approximately in the basal 4/5 part of the truncus (Fig. 14a). Its single central tendon terminates at the ventral base of the glans and functions in flexing the glans by approximately 90° against the shaft so that in a flexed position the glans is orientated parallel to the shaft in a distal prolongation (Fig. 14e). Particularly the base of the truncus is heavily sclerotised (Figs. 14b, c) and bears two dorsally curved lateral projections as attachment sites for both the posterior and anterior pairs of extrinsic penial muscles (101 and 102 in Fig. 14b). In resting position the posterior extrinsic muscles pass ventrally of the pregenital chamber, are folded and attach to tergites XIV+XV, at both sides of the anal operculum. Dorsodistally the truncus is

provided with an oval shaped internal cavity, opening to the exterior via a large median slit, which is also confirmed by cross sections (Fig. 14d). The proximal and distal slit areas are sclerotised. A pair of accessory glands is present with ducts connected to the sheath of the pregenital chamber (Fig. 14b). The glans bears two pairs of sensilla chaetica, its stylus is provided ventrally with a brush of setae and dorsally with two or three pairs of minute denticles (Figs. 14e, f). The sensilla chaetica as well as the brush setae appear to be innervated, indicating that the brush may also have a sensory function.

The female reproductive apparatus consists of an inner and outer sheath enclosing an ovipositor, which is a dorsoventrally flattened cylinder composed of 25 to 27 cuticular annulations, terminating in a bifurcate tip consisting of three apical rings (Figs. 14g, h). At the furca base the vagina marks the distal end of the uterus internus. The proximal ovipositor segments 7 and 8 have two pairs of sensilla chaetica, followed by 14 to 16 segments with four pairs, while the distal furca segments have 4, 6 and 16 sensilla chaetica on each side respectively. On the distal segment a rounded projection is situated, provided with a tuft of sensory setae (Fig. 14h), probably deriving from a single sensillum chaeticum (Martens et al. 1981). The second rings have two pairs of two slit sensilla on the dorsal, and two pairs on the ventral side. At the level of the distal 5th to 7th ovipositor segments the seminal receptacles are located (Figs. 14h, i).

The base of the pregenital chamber is provided with a pair of posterior extrinsic genital muscles at-

Tab. 5: Average totals of sensilla basiconica, falciform setae, solenidia and spines for one male and one female.

	Basiconica		Falciform setae		Solenidia		Spines	
	Male	Female	Male	Female	Male	Female	Male	Female
Pedipalp	13	13	10	13	43	44	2	2
Leg I	8	10	13	14	40	46	44	46
Leg II	15	19	17	17	62	61	8	8
Leg III	8	8	8	8	25	26	56	54
Leg IV	9	9	6	7	22	21	80	74
Totals for one animal	106	118	108	118	384	396	380	368

taching to tergites XIV+XV. Another pair of muscles derives from the base of the pregenital chamber, enclosing the outer sheath dorsally and ventrally as a single sheet of muscle fibres and then joining with the muscles of the anterior genital muscle that attaches to the lateral plaques of sternite VIII (Fig. 14g).

Conclusions and discussion

Much work has been done on the basic morphology, distribution and ultrastructure of sensory structures in several arachnid groups, such as Ricinulei (Talarico et al. 2006, 2008) and Acari (Coons & Alberti 1999). For Opiliones only a limited number of studies have been published on this matter. Since the ultrastructure of campaniform sensilla, falciform setae, sensilla basiconica, solenidia and bipterate setae has not been examined in Opiliones so far, their functional properties have not been established. Willemart & Giribet (2010) proved that the shaft of solenidia has a multipored nature, indicating that they are olfactory sensilla (reviewed in Willemart et al. 2009). They show similarities to 'Type 6' sensilla in Ricinulei

(Talarico et al. 2006). At least some sensilla chaetica have a terminal pore (Willemart & Gnaspini 2003) which would fit the view that these sensilla chaetica are contact chemoreceptors or have a dual function (contact chemoreception and mechanoreception) (Guffey et al. 2000, Kauri 1989, Spicer 1987, Willemart & Gnaspini 2003, Willemart et al. 2009). It appears that trichomes are non-sensory hairs for which several functions have been proposed: they may protect the integument as well as other sensilla and act as a brush to clean the body (Willemart & Gnaspini 2003, Willemart et al. 2009).

The best studied sensory type is the slit sensillum (Barth & Stagl 1976, Barth 2002, 2004, Blickhan & Barth 1985, Kropf 1998, Luque 1993, Talarico et al. 2006, 2008). Slit sense organs are known to be detectors of mechanical stresses in the cuticle caused by muscular activity and/or haemolymph pressure (proprioception), or of strains imposed by external pressure (exteroception; Barth 2004, Shultz & Pinto-da-Rocha 2007). In *D. ramosus*, for example, the single slit sensillum close to the tip of the pedipalpal

Tab. 6: Summary of sexual dimorphism in *D. ramosus* (differences in colouration not included).

	Male	Female
Opisthosoma	Small, flattened dorsally	Large, with dorsal protuberance
Pedipalp	Length 6.5 mm; Femur, patella and tibia no plumose setae; Patellal apophysis slender with more pointed tip, covered with sensilla chaetica only; Tarsus with ~10.2 campaniform sensilla; Tarsus with ~9.6 falciform setae	Length 6.8 mm; Femur, patella and tibia with plumose setae; Patellal apophysis stout with more rounded tip, covered with plumose setae only; Tarsus with ~15.4 campaniform sensilla; Tarsus with ~12.5 falciform setae
Legs	Longer (Tab. 2); Tarsus I with ~31.2 solenidia; Tarsus I with ~4.3, tarsus II with ~9.2 basiconica; Leg III and IV with bipterate setae; Tarsus IV with ~30.5 pairs of spines	Shorter (Tab. 2); Tarsus I with ~37.0 solenidia; Tarsus I with ~6.4, tarsus II with ~12.6 basiconica; Leg III and IV without bipterate setae; Tarsus IV with ~27.4 pairs of spines

tarsus (Fig. 7a) probably senses torsion forces caused by the use of the pedipalpal claw. This is very similar in Ricinulei (Talarico et al. 2008).

The ventral side of the body has a higher density of slits than the dorsal side (Tab. 4; sternites plus genital operculum app. 94 slits, carapace plus tergites app. 60 slits; compare Figs. 13a, h, i) which is most likely related to the ventral presence of reproductive organs. The occurrence of sternal slit sensilla (Fig. 13h) clearly coincides with insertion plaques of various muscle groups that are involved in everting/inverting the penis/ovipositor: the extrinsic genital muscles directly operate the genital tract, whereas the lateral longitudinal muscles regulate opisthosomal volume and haemocoelic pressure (Barth 2004, Martens et al. 1981, Shultz 2000). Consequently, the slits on the genital operculum and ventrum probably function as detectors of cuticle deformations once the genital operculum is opened and the penis or ovipositor is extruding. Thus, for both sexes they may play an essential proprioceptive sensory role during courtship and mating activities. In addition, for the female these slits may be functional during egg deposition.

The slit sensilla on the lateral margins of the dorsal prosoma occur associated with muscle insertion plaques that are involved in movements of the leg coxae (Fig. 13i; pedal tergocoxal muscles no. 65 to 69 in Shultz 2000). I traced only one publication relating to slit sensilla and muscle insertion plaques. Referring to single slits in spiders, Barth (2002, p. 41) mentioned that "some of them lie conspicuously close to the sites of muscle attachment".

Although no histological studies on campaniform sensilla have been conducted so far, most authors regard them as homologous to slit sensilla, detecting mechanical stresses in the cuticle (Edgar 1963, Barth & Stagl 1976); a view which is supported by this study. In *D. ramosus* they appear in four groups on the proximal leg femora, exactly at sites where in *Amilenus aurantiacus* (Simon, 1881) (Phalangiidae) slit groups are located (Barth & Stagl 1976). Also, their orientations relative to each other and – generally – perpendicular to the long axis of the appendages are similar. Some of these similarities have previously been pointed out by Barth & Stagl (1976). Moreover, on the leg metatarsi groups are composed of typical campaniform sensilla together with slit-like types and intermediary shapes not clearly attributable to either category, as was also recorded by Edgar

(1963). Campaniform sensilla may be characterised as 'compact slits'.

The row of campaniform sensilla laterally on the pedipalpal tarsus (Figs. 8e, 9f) may communicate to the animal how much mechanical resistance is offered by a particular surface the harvestman is probing, e.g. the hardness/softness of a potential food item. The larger numbers on the female pedipalpal tarsus (Tab. 1: male 10.2, female 15.4 campaniform sensilla) may play a role in selecting suitable egg deposition sites.

When dealing with 'proprioceptive organs' in Opiliones, slit and campaniform sensilla may deserve identical treatment. In a comparative study on slit sensilla in the legs of Chelicerata, Barth & Stagl (1976) excluded campaniform sensilla distal to the femur of *Amilenus aurantiacus*, and consequently made mention of only 45 slits for leg I. In *D. ramosus* an average of 52 slits and 104 campaniform sensilla were recorded for leg I (Tab. 4), which results in a considerably larger total of 156 'proprioceptive' sensilla on leg I. Total numbers for one male are 866 (410 slits + 456 campaniform sensilla); for one female 884 (418 slits + 466 campaniform sensilla), of which 628 (73% and 71% respectively) are located in the legs.

The legs in *D. ramosus* – and Eupnoi in general – easily break off at the appendotomy plane, at the trochanter-femur junction. A leg can be actively detached to escape from a predator, or in case it is trapped during moulting (Edgar 1963). As these legs are not regenerated, it is common to encounter harvestmen in the field with one or more legs missing. In *D. ramosus* all legs have a similar basic set of sensory structures like sensilla chaetica, solenidia, falciform setae and sensilla basiconica. So, the loss of one or more legs does not fundamentally affect the sensory capabilities.

The highest numbers occur on the first and second legs, indicating that these legs have an important sensory function (Tab. 3). Compared to legs III and IV, legs I and II have larger numbers of sensilla chaetica in the ventral region of the tarsi (Fig. 12, Tab. 3), which may be associated with a more accurate perception of the physical characteristics of the environment like size, form and texture (Willemart & Gnaspini 2003).

Judged only from the numbers of solenidia (male app. 52, female 51), leg II is the most important sensory organ, but considering its extreme length, its

tarsus has a rather low density of solenidia per mm (male app. 2.2, female 2.7), whereas the tarsus of leg I (male app. 31, female 37 solenidia) is much shorter, resulting in a density of 3.6 and 5.1 solenidia per mm, respectively. This also applies for basiconica and falciform setae. With leg II the animal can obtain 'general features' of its wider surroundings, whereas leg I is more appropriate for gathering detailed information at closer range. This strongly supports the recent point of view to reconsider the general denomination of 'sensory appendages' for legs II in Opiliones (Willemart & Gnaspini 2003, Willemart & Chelini 2007, Willemart et al. 2009).

The absence of spines on the tarsomeres of leg II may facilitate grooming of these appendages, thus cleaning the sensory organs, in cooperation with the chelicerae, pedipalps and mouth; a behaviour that is often seen in this species. Spines occur on the proximal tarsomeres of legs I, III and IV, lacking in the distal regions (Fig. 10) which are often observed to be tightly wrapped around grasses or other objects to anchor themselves to a substrate (Guffey et al. 2000).

The pedipalps are loaded with densely arranged sensilla (up to 34 solenidia on the tarsus measuring about 1.8 mm) with higher densities towards the tarsal tip (Figs. 7a, b) and they are therefore very important sensory organs. The distribution of sensilla shows remarkable similarities with the pedipalp of Ricinulei (Talarico et al. 2008: Fig. 5). In *D. ramosus* the contact mechano- and chemoreceptors (sensilla chaetica) are scattered over the whole surface for optimum exposure to all surfaces the animal explores by touch. But the solenidia and sensilla basiconica occur only in the dorsal to dorsolateral region, away from potentially contaminating substrata (like sticky food items or moist substrates), and protected from direct contact by a cover of trichomes (Fig. 7c). These sensilla may work once a substratum is actively touched with the dorsal region of the pedipalpal tarsus, a behaviour that is often seen in the field (e.g. Fig. 1). Willemart & Hebets (2012) recorded this 'pedipalp tapping' (a behaviour wherein the tip and the dorsal region of the tarsi gently touch the substrate) in *Leiobunum vittatum* (Say, 1821) (Sclerosomatidae). They found that both males and females react by pedipalp tapping to chemical cues left on a substrate by conspecifics. This suggests that besides sensilla chaetica one or more of the other sensilla types (e.g. basiconica, falciform setae or the basiconica 'trident') on the dorsal pedipalpal region may have a chemoreceptive function.

Interestingly, in some cases two different sensory structures occur 'clustered': a slit group with a group of solenidia on the pedipalpal femur (Figs. 8c, j, 9c), a bifid metatarsal spine associated with a single slit sensillum in the legs (Fig. 11), solenidia and campaniform sensilla proximally on the leg femora (Fig. 10). Whether these sensilla combinations represent specialised functions remains to be studied.

In general, the results show a remarkable similarity between males and females in the topography and number of examined sensilla (Tabs. 4, 5, 6). The pedipalpal tarsus, for example, has not revealed any significant macro- or microsculptural sexual disparity, except for the larger numbers of tarsal campaniform sensilla and falciform setae in the female.

Both sexes have equivalent numbers of leg sensilla (Tab. 3), but the female has more basiconica in legs I and II, and more solenidia in legs I. The male leg IV has slightly more spines. However, since the female's legs are much shorter this results in higher densities of sensilla for the female. This is most distinct for basiconica densities in legs I and II and for solenidia densities in leg I.

A very evident result concerning sexual dimorphism in *D. ramosus* is the female pedipalp which is covered with hundreds of plumose glandular setae, absent in the male, whereas the male has hundreds of bipterate setae on legs III and IV, absent in the female. Until now bipterate setae had been found only in *Phalangium opilio* (Willemart et al. 2009). For comparison, I investigated some specimens of *P. opilio* and found bipterate setae on the male legs III and IV, with very similar morphology, topography and densities as in *D. ramosus*. I failed to find them in legs I and II. It should be mentioned here that the SEM micrographs in Willemart et al. (2009: Figs. 9, 10, 11) show distorted bipterate setae, with winged portions twisted, not representing their natural arrangements as seen with light microscopy. This is likely a result of procedures for scanning electron microscope preparations.

The morphology of bipterate setae suggests that they are olfactory sensilla. Both wings of each seta are concavely shaped, and their striae are directed towards the proximal junction, possibly 'guiding' odour molecules to the micropore. Their arrangement on the dorsal and anterodorsal leg surfaces provides optimum exposure to the atmosphere, and thus, to

odorant stimuli that arrive at the animal's legs from ahead. As this character is sexually dimorphic, the function of bipterate setae may be to detect a female from a distance and direct him towards her. Non-tactile perception of volatile secretions has been demonstrated in Goniosomatinae (Gonyleptidae) (Machado et al. 2002). A cotton swab with exocrine gland secretions of the same species held at a distance of 1–2 cm from an aggregation elicited an alarm response. Whether the volatile secretions receptive to the male of *D. ramosus* are produced by the glandular plumose setae of the female remains to be tested.

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